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Differences In Post-Emergence Growth Of Three Fern Species Could Help Explain Their Varying Local Abundance

KAI RÜNK* and MARTIN ZOBEL

Institute of Ecology and Earth Sciences, Department of Botany, University of Tartu, 40 Lai St., 51005 Tartu, Estonia

ABSTRACT.—Despite the large number of comparative studies on species with different distribution and abundance, no clear general pattern of attributes explaining species' rarity has yet been found. The relationship between different life-history traits of a species and abundance tend to be conditional and context dependent. We were interested in whether the local relative population density of three fern species in Estonia is related to post-emergence growth of their young sporophytes, i.e., that the locally abundant species, *D. carthusiana*, has the highest vegetative growth in its first growth periods and the two less abundant species, *D. dilatata* and *D. expansa*, have lower. We were also interested in differences between generative traits of young sporophytes of three species, specifically in the number of spores. We grew the species in a garden experiment for two vegetation periods, 2004–2005, until the first sporulation. The relative population density of the three *Dryopteris* species was related to the relative post-emergence growth of the species. The most abundant species *D. carthusiana*, exhibited the highest values of vegetative growth parameters in the first growth period. The less abundant *D. dilatata* and *D. expansa* both had shorter fronds, shorter intensive growth periods and lower leaf elongation rates. *Dryopteris dilatata* had a different vegetative growth strategy compared to the other two species; it differed in timing of intensive growth of frond length and increase of frond number and had the lowest values of generative parameters among the three species.

KEY WORDS.—*Dryopteris*, Post-emergence growth, Rarity

Ecology is aimed at detecting factors and processes that control the relative abundance and distribution of species (Kunin and Gaston, 1997; Crawley, 1997). Understanding why some species are more common than others provides us with basic information about the distribution and regional dynamics of different species. Such understanding is essential for the practical conservation and management of rare species, i.e., species with a low relative abundance/distribution at continental, and particularly at regional and local levels.

One possible approach for investigating the mechanisms behind rarity is through the comparison of taxa with contrastingly different distribution and abundance patterns (e.g., Baskauf and Eicmeier, 1994; Sultan, 2001; Simon and Hay, 2003; Pohlman *et al.*, 2005). The study of pairs or even larger numbers of closely related taxa with common genetic heritage may more easily reveal factors limiting rare species (Baskin and Baskin, 1986; Silvertown and Dodd,

* Corresponding Author: (E-mail: kai.runk@ut.ee; phone: +3727376381; fax: +3727376222)

1996; Gitzendanner and Soltis, 2000). Despite a large number of comparative studies on the subject (e.g., reviewed in Bevill and Louda, 1999; Binney and Bradfield, 2000; Brown *et al.*, 2003; Rymer *et al.*, 2005), no clear pattern of general attributes or one specific feature explaining species' rarity has yet been found. Relationships between different life-history traits of a species and abundance tend to be conditional and context dependent (Murray *et al.*, 2002).

Several recent studies have focused on the relative importance of dispersal and environmental determinants of fern distribution. Evidence has been found that habitat availability, at a local scale (Richard *et al.*, 2000; Wild and Gagnon, 2005) and a regional scale (Guo *et al.*, 2003), and not dispersal capability is responsible for fern distribution. Karst *et al.*'s study (2005) at two contrasting local spatial scales (local mesoscale and local fine) showed that fern distribution at the local mesoscale (135–3515 m) was linked to environmental factors, but at the local fine scale (4–134 m); both dispersal and abiotic environment were jointly responsible for fern distribution.

Comparative studies of the different life phases of fern ecology (spores, gametophytes and sporophytes) have shown the different amplitude of the abiotic factors under study. Although this amplitude is usually broader in the case of spores (compared with gametophytes; Hill, 1971; Prada *et al.*, 1995) and gametophytes (compared with sporophytes; Sato and Sakai, 1981), the persistence of fern species in a habitat is possible only if the realized niches of spores, gametophytes and sporophytes match. A habitat that meets requirements of gametophytes or young sporophytes may be less or not at all suitable for mature sporophytes. Consequently the early period of sporophyte generation, then vascular sporophyte emergences from a small non-vascular gametophyte (Page, 2002) is extremely important in the life of a fern species. For this reason traits of post-emergence growth (Leishman, 1999) of young sporophytes could be particularly important for the performance of a species and determine distribution. The degree of influence of resource availability in the pertinent location on the success of early growth of young sporophytes' is known to be high (Grime, 1985) and may to a great extent depend on competitive pressure of surrounding neighbors (Cousens, 1981; Grime *et al.*, 1988; Rünk *et al.*, 2006).

The current study is a part of a larger project investigating the possible reasons of different regional frequency and local abundance of three closely related co-occurring fern species: *Dryopteris carthusiana*, *Dryopteris expansa* and *Dryopteris dilatata*. *Dryopteris carthusiana* is common in Estonia; *D. expansa* is distributed in scattered localities throughout Estonia, while *D. dilatata* is rare, being close to its north-eastern distribution limit. According to our earlier study (Rünk *et al.*, 2004); the different competitive abilities of *D. carthusiana* and *D. expansa* might help explain their different relative regional frequency, but not in the case of *D. dilatata*, which is near its distribution border as tolerant to competition as the most frequent *D. carthusiana*. Climatic factors are a likely limitation to distribution of *D. dilatata* in Estonia. The northern distribution limit of this species is approximately 300 km from Estonia, in southern Finland (Hultén and Fries, 1986), and shadows the

isothermal line along which the coldest month is between 5 and 8°C (Boucher, 1987). Still, the particular mechanism behind climatic restrictions remains open to debate.

The results of field survey of the three species on permanent plots showed the higher local relative population density of *D. carthusiana* compared to *D. dilatata* and *D. expansa* (Rünk *et al.*, 2006). The order of the species' rankings could be explained by the competitive ability of the three fern species.

Therefore we hypothesized that the local relative population density of the three fern species is related to the success of post-emergence growth of their young sporophytes, i.e., that comparatively more abundant species have the highest vegetative growth in their first growth periods. We were also interested in whether there were differences in the generative traits of the three species' young sporophytes, and erected the hypothesis that *D. dilatata* had the lowest number of spores than *D. carthusiana* and *D. expansa*.

Material and Methods

Study species.—The three species studied are closely related from an evolutionary point of view (Gibby and Walker, 1977) and are morphologically similar (Fraser-Jenkins and Reichstein, 1984; Page, 1997). All three species are medium-sized, rhizomatous, herbaceous plants with 3-pinnate fronds and orbicular sori covered with reniform indusia (Fraser-Jenkins, 1993). Tetraploid (2n = 164) *Dryopteris carthusiana* (Vill.) H.P. Fuchs is the most common of the three species, and can be found throughout Europe, North America, West and Southeast Asia (Hultén and Fries, 1986; Fraser-Jenkins, 1993). *Dryopteris expansa* (C. Presl) Fraser-Jenkins and Jermy can also be found in North America and Asia. Tetraploid (2n = 164) *Dryopteris dilatata* (Hoffm.) A. Gray is distributed mostly in Western and Central Europe (Hultén and Fries, 1986; Fraser-Jenkins, 1993). Diploid (2n = 82) *D. expansa* is mainly restricted to mountainous regions of Europe, and has a more northerly and easterly distribution than *D. dilatata* (Fraser-Jenkins and Reichstein, 1984; Hultén and Fries, 1986). Piękoś-Mirkova (1991) found *D. expansa* at 2098 meters above sea level, above the timberline in the Poland's Tatra Mountains. In Scandinavia, the distribution limit of *D. expansa* is the northernmost of the three species (Jonsell, 2000). In Western and Central Europe, *D. dilatata* is a more common species than *D. expansa* (Fraser-Jenkins and Reichstein, 1984; Page, 1997). In Estonia the opposite is true; *D. expansa* is distributed in scattered localities throughout Estonia (Kukk and Kull, 2005), while *D. dilatata*, close to its north-eastern distribution limit (Page, 1997; Jonsell, 2000), is rare. *Dryopteris carthusiana* possesses the highest regional frequency of the three species, and is evenly distributed across the country. Similarly, the local abundance (population density) of *D. carthusiana* is the highest among the three species (Rünk *et al.*, 2006). According to the Atlas of the Estonian Flora (Kukk and Kull, 2005), in which Estonia is divided into a grid of 513 (6 × 10 minute squares), D. carthusiana was recorded in 441, *D. expansa* in 145 and D. dilatata in 20 of the squares. While *D. expansa*, like *D. carthusiana*, is distributed

evenly, most of *D. dilatata* populations are situated in the northern and western part of the country. In Estonia all the species can be found growing in mesic woodlands (Rünk, 2002), mostly in mixed populations.

All three fern species (*D. carthusiana*, *D. dilatata* and *D. expansa*) are sexually reproducing species (Manton, 1950) with sporangia that contain 64 spores (Widén *et al.*, 1967; Schneller, 1975; Fraser-Jenkins and Reichstein, 1984) with a similar size per sporangium (Piękoś-Mirkova, 1979; Seifert, 1992). Species nomenclature follows Fraser-Jenkins (1993).

Experimental design.—Vegetative growth, reproduction, morphology and biomass were assessed in a common garden experiment conducted in 2004 and 2005. Spores of all fern species were collected in the wild in July 2003 and stored in a refrigerator (at 2 ± 1°C) until the beginning of the experiment. The substrate used for spore germination was sterilized and consisted of 3 parts horticultural peat and 1 part fine-grade sand. Spores were sown on October 20, 2003 and sporophytes emerged in March 2004. Young sporophytes were planted, nine evenly spaced per plastic box (12 × 8 × 8 cm deep), on May 16, 2004. The specimens were replanted individually in plastic pots (10 cm diameter, 8 cm deep) on August 2. Initially all three species were represented by 60 individuals, but for the final harvest and analysis, 15 individuals per species were randomly selected.

The soil mixture used for receiving sporophyte plants consisted of 4 parts horticultural peat and 1 part fine-grade sand. The boxes were placed in a greenhouse at 22 ± 2°C with a photoperiod of 12:12 h (fluorescent light: daylight tubes, photon flux density 40 μmol $s^{-1}m^{-2}$) and watered as needed to keep the soil moist. On August 10 the pots were relocated to the experimental garden and grown in shaded light for another 14 months. In order to minimize possible differences in illumination, the positions of all pots were changed weekly. To imitate the species' natural Estonian environment a screen with a shade value of 65% was used, as all three species can be found growing mainly in mesic woodlands. Shade treatment was provided using a screen made of aluminum-coated shade cloth (spectrum neutral; Ludvig Svensson, Kinna, Sweden). During the winter of 2004/2005, plants were covered with horticultural peat imitating fallen leaves and their decayed remnants.

The experimental garden was located in Tartu (58°21′25″N, 26°42′5″E, 68 meters a.s.l.), in south-eastern Estonia, where the average annual temperature is 5.0°C and the average amount of annual precipitation is 550 mm (Jaagus, 1999).

Data collection.—During the two growing seasons, a total of nine measurements were conducted every 28–34 days. Five measurements were made in 2004 (on June 9, July 9, August 9, September 10, October 8) and four in 2005 (on June 22, July 27, August 25, September 30), the first measurement of each year occurring when the fronds had rolled out and the last just before the first autumn frost. For each individual, the number of fronds was counted and the length of the longest frond was measured. In generative individuals, the number of fertile (spore-bearing) fronds was also counted. In the case of the length of the longest frond the frond was measured to the nearest millimeter on

each individual fern between the base of the stipe (stalk of the frond) and the tip. Those measurements allowed us to calculate leaf elongation rate (LER) and frond number increase rate (NIR).

Leaf elongation rate (LER, mm/day) were calculated using the following basic equation:

$$\mathrm{LER} = \frac{(M_{n+1} - M_n)}{D} \quad (1)$$

where M_{n+1} is the current measurement in millimeters; M_n is the previous measurement in millimeters and D is the number of days between measurements.

Frond number increase rate (NIR, number of fronds/day) was calculated using the following basic equation:

$$\mathrm{NIR} = \frac{(F_{n+1} - F_n)}{D} \quad (2)$$

where F_{n+1} is current measurement (number of fronds); F_n is the previous measurement (number of fronds); D is the number of days between measurements.

LER and NIR were calculated for all seven time intervals between the measurements; four in 2004 (June, July, August and September) and three in 2005 (July, August and September). In generative individuals, the number of fertile (spore-bearing) fronds was also counted.

After the final harvest in October 2005, fronds, rhizomes and roots were separated and dried at 75°C for 48 hours. Biomass fractions were determined by weighing the parts separately. The length of all fronds and frond laminae (the leafy part of the frond) were measured to the nearest millimeter before the final harvest. The length of the stipe was obtained by subtracting lamina length from frond length. Lamina area and lamina area (pinnae) covered with sori were measured using a scanner (ScanJet5p), DeskScan II 2.9, and Pindala 1.0 software (designed by I. Kalamees, Eesti Loodusfoto, Tartu, Estonia). Specific leaf area (SLA) was calculated as lamina area (cm^2) per unit of lamina dry mass (g).

Statistical analysis.—Differences in and the timing of vegetative growth (length of the longest frond and the number of fronds) during the both growth periods were tested separately for each year with repeated measures of ANOVA (using the Statistica software version 6.0; StatSoft Inc., 1998) with the species (three levels) as fixed factors and measurement time (five levels in 2004 and four levels in 2005) as a repeated factor.

Differences in vegetative growth rate, LER and NIR, between *D. carthusiana*, *D. dilatata* and *D. expansa* during the growth periods in the years 2004 and 2005 were tested separately for each year with repeated measures of ANOVA with the species (three levels) as fixed factors and period of time between measurements (four levels in 2004 and three levels in 2005) as a repeated measurement factor.

TABLE 1. Results of repeated measures ANOVA: effects of species, measurement time and their interaction on the length of the longest frond and on the number of fronds of *Dryopteris carthusiana, D. expansa* and *D. dilatata* in 2004 and in 2005.

Source of variation	Species			Time			Species*time		
	Df	F	P	Df	F-ratio	P	Df	F	P
Length of the longest frond in 2004	2	5.315	0.009	4	414.98	<0.000	8	12.63	<0.000
Length of the longest frond in 2005	2	9.448	<0.000	3	532.35	<0.000	6	5.937	<0.000
Number of fronds in 2004	2	21.88	<0.000	4	418.52	<0.000	8	4.865	<0.000
Number of fronds in 2005	2	11.88	<0.000	3	251.58	<0.000	6	1.508	0.181

Differences in the length of the longest frond and the number of fronds at the end of both growth periods and other morphological, biomass and reproductive parameters between *D. carthusiana*, *D. dilatata* and *D. expansa* at the end of the experiment were tested by one-way ANOVA with the species (three levels) as fixed factors. In the case of LER and NIR the equation $X' = \sqrt{X} + \sqrt{X} + 1$ was used for transformation (Zar, 1999). All other variables were log transformed, except in the case of relative biomass allocation, for which the data (as proportions) was arcsine square root transformed.

Differences between mean number and length of fertile and sterile fronds among species were tested by Students' t-test. The significance of the differences among all other parameters means was estimated with a Tukey HSD multiple-comparison test with a 0.05 significance level (Sokal and Rohlf, 1995).

RESULTS

Vegetative Growth Traits

Vegetative growth and timing of the vegetative growth.—During both growth periods in 2004 and 2005, there were differences in length of the longest frond and in number of fronds between the three species (Table 1). *Dryopteris carthusiana* and *D. dilatata* were characterized by longer fronds and by a higher number of fronds than *D. expansa*; all differences were significant except in the case of the length of fronds between *D. dilatata* and *D. expansa* in 2004. There were also differences in the timing of vegetative growth between the species in 2004 and 2005 (Table 1), except in the case of the number of fronds in 2005. In 2004, *D. carthusiana* had the longest period of intensive growth when the increase in number of fronds and length of the longest frond between measurements were significant. The production of new fronds and the growth of the longest frond continued until September. *Dryopteris expansa* had the shortest period of intensive growth of the three species; the number of leaves increased until August and the length of the longest frond increased only until July. *Dryopteris dilatata* produced new fronds even in September, however the growth period of the longest frond matched that of *D. expansa*; it took place only in June.

TABLE 2. Results of repeated measures ANOVA: effects of species, period of time between measurements and their interaction on the LER and NIR of *Dryopteris carthusiana*, *D. expansa* and *D. dilatata* in 2004 and 2005.

Source of variation	Species			Time period			Species* time period		
	Df	F	P	Df	F	P	Df	F	P
LER 2004	2	22.66	<0.000	3	42.73	<0.000	6	4.704	<0.000
LER 2005	2	8.181	0.001	2	70.03	<0.000	4	0.848	0.499
NIR 2004	2	7.000	0.003	3	10.15	<0.000	6	1.638	0.144
NIR 2005	2	11.81	<0.000	2	17.53	<0.000	4	1.264	0.291

LER (leaf elongation rate) and NIR (fronds number increase rate).— Differences in LER (Table 2, Fig. 1) were more distinct than in growth of the longest frond or number of fronds; *D. carthusiana* had significantly the highest LER in 2004 and *D. dilatata* in 2005; the differences between the other two species were non-significant in both years. The timing of LER was different only in 2004; *D. carthusiana* had significantly higher LER in August 2004, compared to the two other species, and in July 2004, compared to *D. dilatata*. There were also differences in LER between 2004 and 2005. At the beginning of the experiment in 2004, LER of *D. expansa* and *D. dilatata* dropped during July, while in the case of *D. carthusiana*, high LER continued up to September.

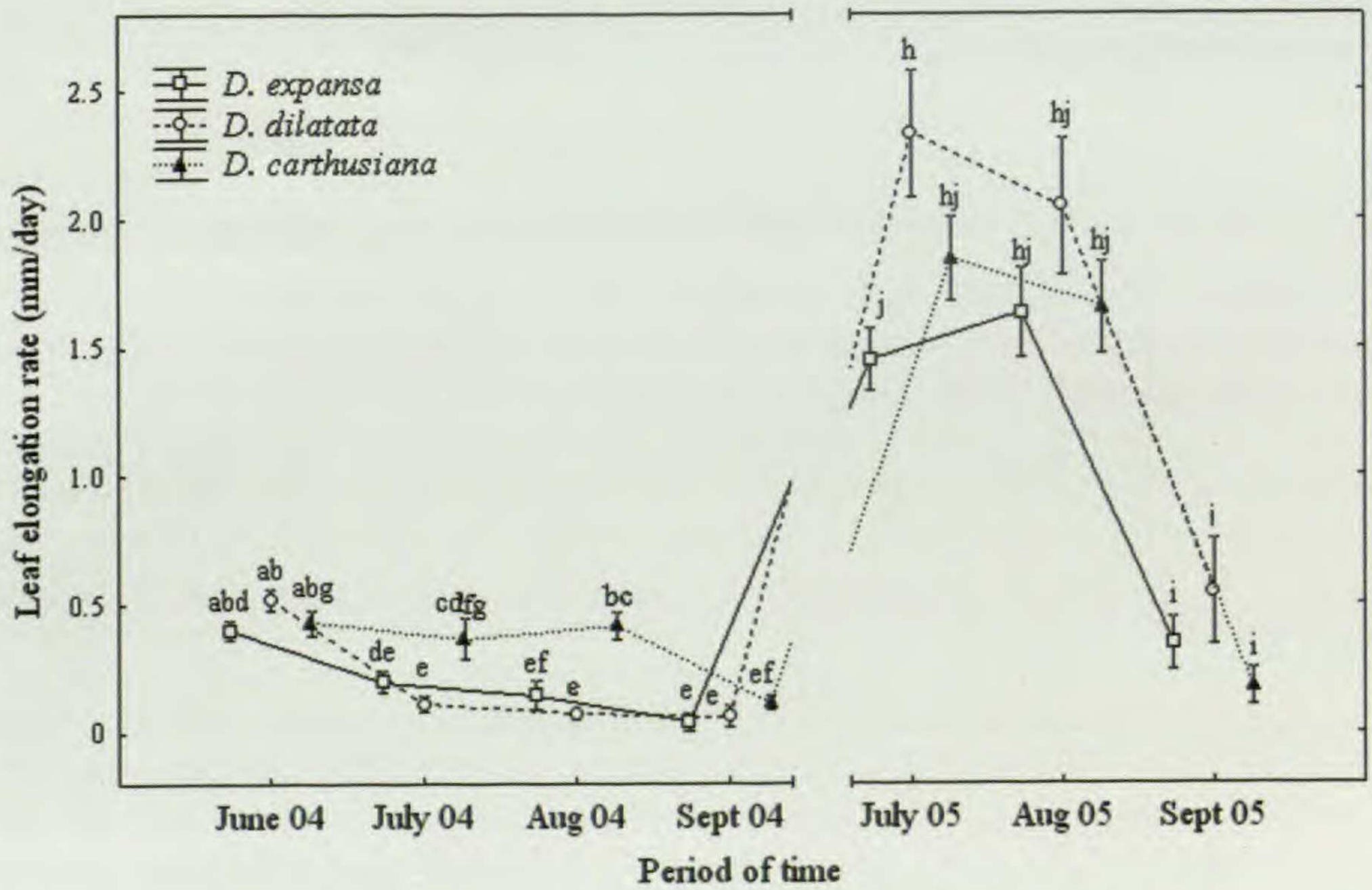

FIG. 1. Mean ± SE of the LER (mm/day) of the longest frond of *Dryopteris expansa*, *D. dilatata* and *D. carthusiana* in June (09/06–09/07), July (09/07–09/08), August (09/08–10/09), September (10/09–08/10) 2004 and in July (22/06–27/07), August (27/07–25/08), September (25/08–30/09) 2005. Whiskers with the same letter are not significantly different ($P < 0.05$, Tukey test; separately for 2004 and 2005). X-axis breaks between the results of different analysis.

TABLE 3. Results of one-way ANOVA: effects of species on the morphological, biomass and reproductive traits of *Dryopteris carthusiana*, *D. expansa* and *D. dilatata* at the end of the first growth period (October 2004) and at the final harvest (September 2005).

	Species (Df = 2)	
Source of variation	F	P
October 2004		
Length of the longest frond	13.60	<0.000
No of fronds	13.52	<0.000
September 2005		
Length of the longest frond	11.72	<0.000
Mean frond length	6.653	0.003
Mean lamina length	4.508	0.017
Mean stipe length	23.93	<0.000
No of fronds	24.54	<0.000
No of fertile fronds	3.754	0.033
No of sterile fronds	12.79	<0.000
Total mass	13.85	<0.000
Rhizome mass	5.968	0.005
Root mass	13.35	<0.000
Frond mass	17.67	<0.000
Relative biomass allocation to lamina	14.20	<0.000
Relative biomass allocation to rhizome	13.97	<0.000
Lamina area	22.91	<0.000
SLA	3.413	0.042
Pinnae area covered with sori	5.472	0.009

In 2005, LER of all three species was the highest at the beginning of the vegetation period and fell significantly in September, at the end of the growth period.

The differences in NIR (Table 2) were similar in both vegetation periods. The increase in number of fronds of *D. carthusiana* and *D. dilatata* was higher than that of *D. expansa*.

Morphological parameters and biomass allocation at the end of growth periods.—The effects of species on the morphological traits and biomass allocation of *D. carthusiana*, *D. expansa* and *D. dilatata* are summarized in Table 3. In October 2004, by the end of the first growth period *D. carthusiana* had the tallest plants (the longest fronds); while two other species were shorter (Fig. 2). By the end of the second growth period (September 2005) *D. dilatata* and *D. carthusiana* both had the longest fronds (Fig. 2). *Dryopteris carthusiana* also had longer fronds (Fig. 2) and stipes than the other two species, and had longer laminae per individual at the end of the experiment (at the final harvest) than *D. expansa*. *Dryopteris expansa* had fewer fronds than other two species in both growth periods (Fig. 3). Fertile fronds of all three species were significantly longer than their sterile fronds (t-test for *D. carthusiana*: $t = -15.42$, $Df = 12$, $P = <0.000$; *D. dilatata*: $t = -7.010$, $Df = 11$, $P = <0.000$ and *D. expansa*: $t = -16.82$, $Df = 13$, $P = <0.000$). *Dryopteris carthusiana* and *D. dilatata* both had significantly higher biomass in regard to all fractions studied

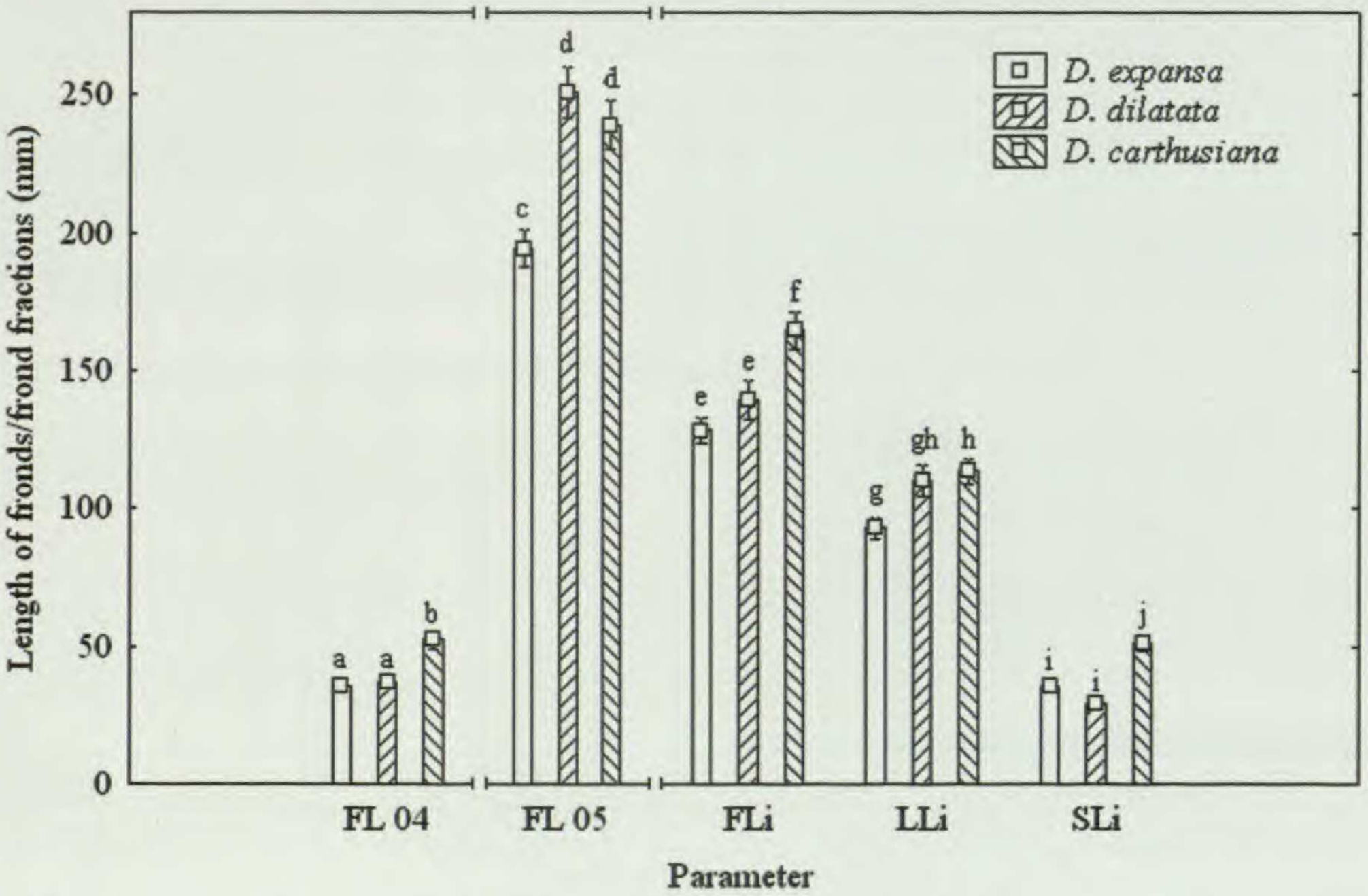

FIG. 2. Mean ± SE of length of fronds of *Dryopteris expansa*, *D. dilatata* and *D. carthusiana*: length of the longest frond in October 2004 (FL 04) and length of the longest frond (FL 05) at the final harvest; length of the fronds (FLi), length of the lamina (LLi) and length of the stipe (SLi) per fern individual (mm) at the final harvest. Bars with the same letter are not significantly different (P < 0.05, Tukey test). X-axis breaks between the results of different analysis.

(total, frond, rhizome and root) and also larger lamina area compared to *D. expansa*. In the case of rhizome mass, the difference between *D. expansa* and *D. dilatata* was marginally non-significant (P = 0.09). There were no differences in SLA between species. The relative biomass allocation pattern was different between species; *D. expansa* allocated significantly more biomass into the rhizome and less into the laminae than *D. dilatata* and *D. carthusiana* (Fig. 4).

Reproductive Traits

Dryopteris dilatata had the lowest proportion of fertile individuals in the final harvest (80.0%), whereas *D. expansa* and *D. carthusiana* had more (93.3% and 86.7% respectively). *Dryopteris dilatata* had significantly fewer fertile fronds compared to the number of its own sterile fronds (t-test: t = 3.178, Df = 11, P = 0.01) and fewer fertile fronds per fertile individual than *D. carthusiana* at the end of the experiment (Fig. 3). *Dryopteris dilatata* also had a smaller pinnae area covered with sori per fertile individual at the final harvest compared to *D. carthusiana* and *D. expansa* (Fig. 5). There was no significant difference between the number of fertile and sterile fronds between the other two species. In the case of *D. carthusiana* and *D. dilatata*, vegetative reproduction was also observed; *D.*

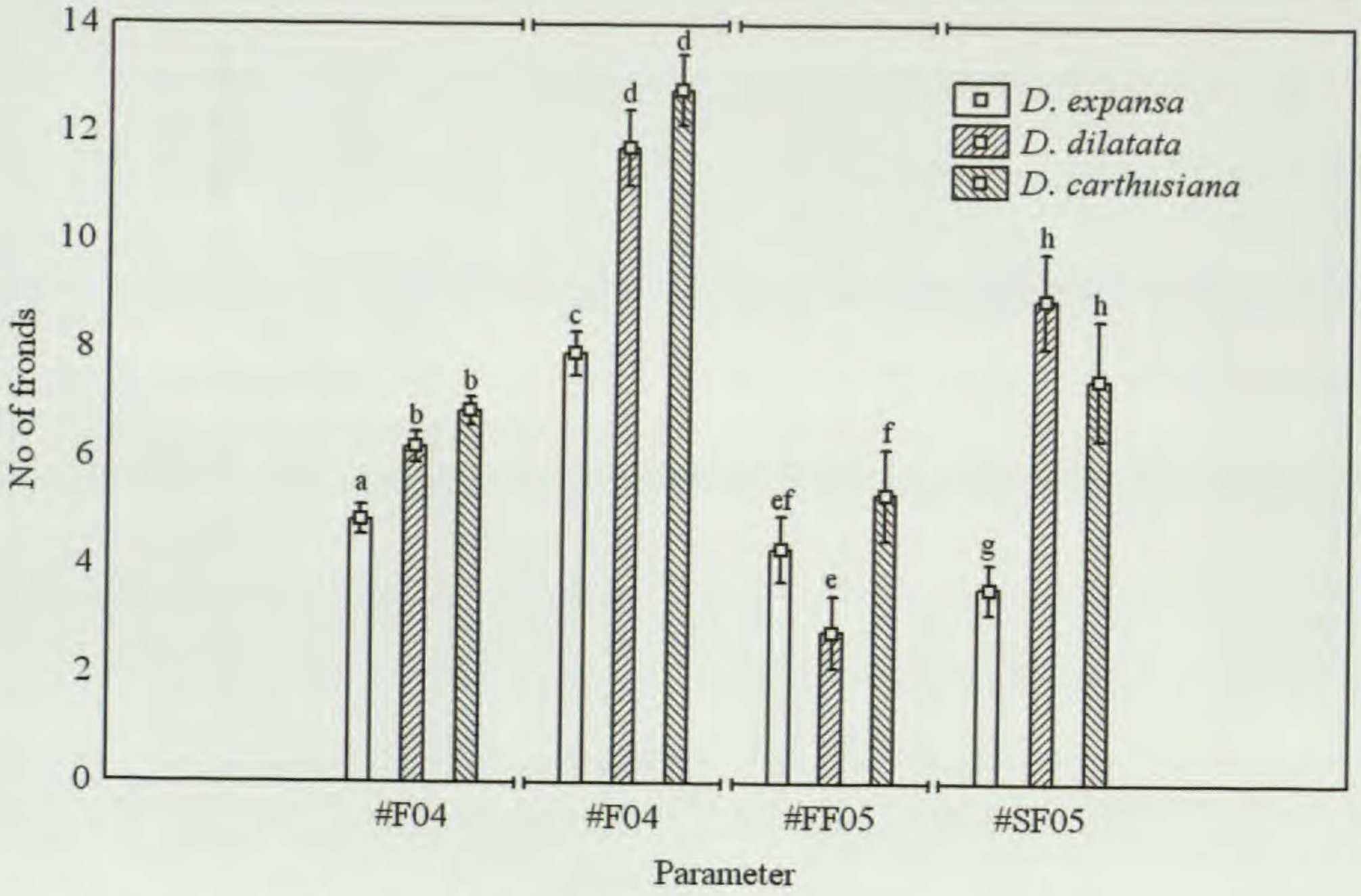

FIG. 3. Mean ± SE of number fronds of *Dryopteris expansa*, *D. dilatata* and *D. carthusiana*: number of fronds per fern individual in October 2004 (#F04), number of fronds (#F05) and number of sterile fronds (#SF 05) per fern individual at the final harvest; number of fertile fronds (#FF05) per generative individual at the final harvest. Bars with the same letter are not significantly different ($p < 0.05$, Tukey test). X-axis breaks between the results of different analysis.

carthusiana had an average of 1.07 vegetative offspring per plant individual and *D. dilatata* 0.07. There was no difference among the species for the time when the first fertile frond appeared; all appeared in August 2005.

DISCUSSION

During the first growth period all three species showed differences in vegetative growth. Intensive growth of *D. carthusiana* for a longer period of time than the other two species resulted in the tallest plants (the longest fronds) by the end of the first growth period and the longest fronds per fern individual by the second growth period. All morphological and biomass parameters, recorded at the end of the experiment, showed that individuals of *D. carthusiana* were larger than those of *D. expansa*. The most successful post-emergence growth may be the crucial precondition for *D. carthusiana*'s high frequency in natural ecosystems. The first vegetation period of young *D. carthusiana* sporophytes was characterized by the longest period of intensive vegetative growth (from June until September), the highest LER, and as a result probably the largest biomass. Achieving higher fertility or utilizing more resources for reproducing could support the finding that the LER of *D. carthusiana* in 2005 was lower than that of *D. dilatata*.

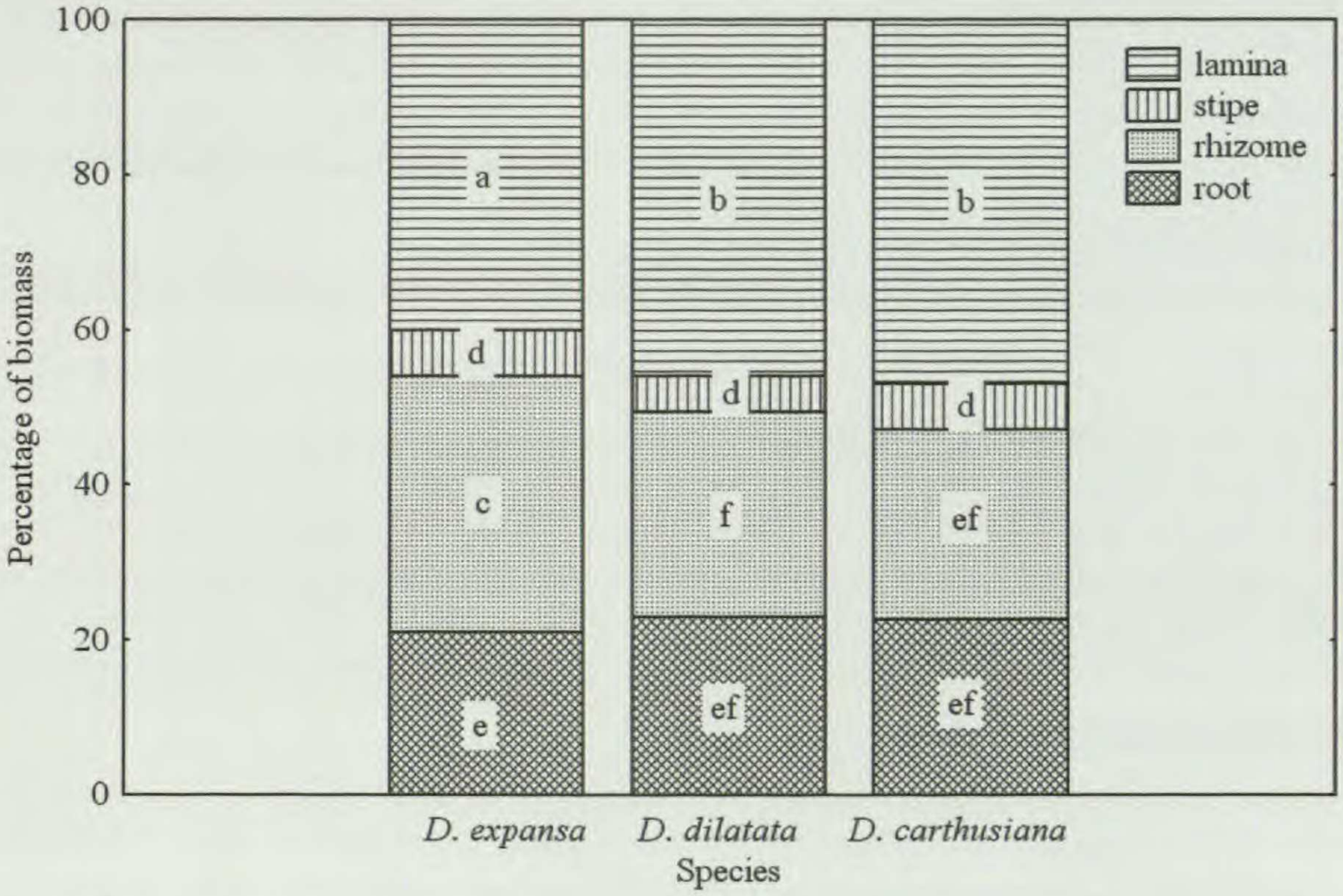

FIG. 4. Mean relative biomass allocation pattern in *Dryopteris carthusiana*, *D. expansa* and *D. dilatata*. Proportions with the same letter are not significantly different ($P < 0.05$, Tukey test).

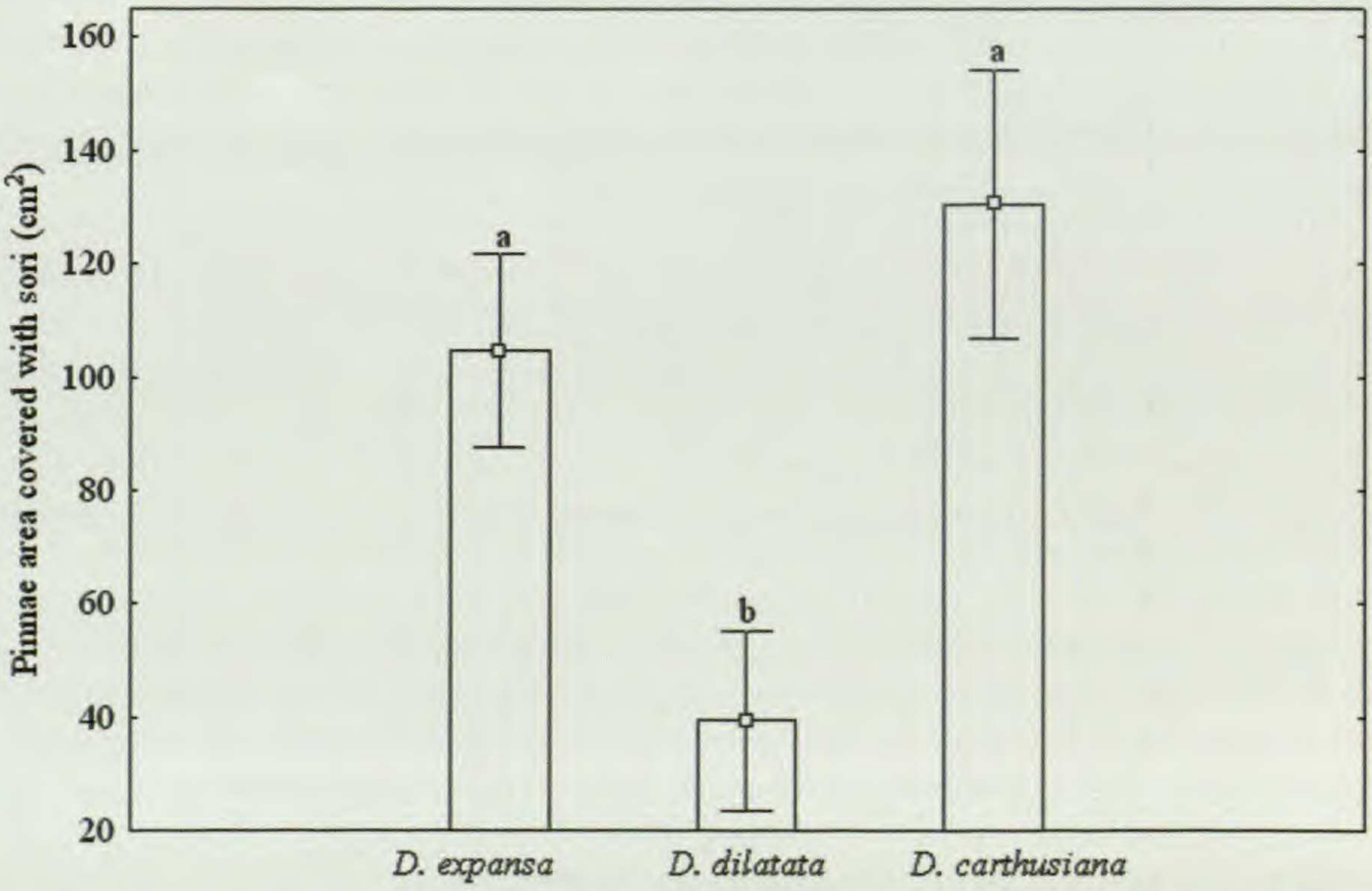

FIG. 5. Mean ± SE of pinnae area covered with sori (cm^2) per generative individual of *Dryopteris expansa*, *D. dilatata* and *D. carthusiana* at the final harvest. Bars with the same letter are not significantly different ($P < 0.05$, Tukey test).

Although none of the reproductive traits of *D. carthusiana* were significantly higher than those of *D. expansa* in the present experiment, the ability of *D. carthusiana* to self-fertilize (in experimental conditions 55% of singly isolated gametophytes grown on soil and even 79% on decomposed wood formed sporophytes; Seifert, 1992) provides the species with a high potential for establishment (Flinn, 2006) and may be an important factor behind its broad distribution. In addition, comparatively high values of vegetative parameters in different light conditions (Rünk and Zobel, 2007), and therefore the high competitive ability (Rünk *et al.*, 2004) may help to explain the highest local (Rünk *et al.*, 2006) and regional frequency (Kukk and Kull, 2005) of *D. carthusiana* among the three species in Estonia.

In the first growth period *D. expansa*, compared to other two species, had the lowest values of frond number parameters (number of fronds in October 2004, increase in number of fronds and NIR in 2004). *Dryopteris expansa*, compared to *D. carthusiana*, had a shorter period of intensive growth, lower LER and lower values of frond growth parameters (length of the longest frond in October 2004 and increase in number of fronds in 2004). The biomass results of the present, two-year experiment related to *D. expansa* were analogous to results of our earlier one-year experiment (Rünk *et al.*, 2004); *D. expansa* had the smallest biomass parameters (total mass, roots mass and frond mass), except in the case of rhizome biomass. We also found a significant difference between *D. expansa* and the other two species in relative biomass allocation, where *D. expansa* invested more biomass in its storage organ, the rhizome, and less in the laminae. The different allocation strategy may be connected with the habitat preferences of this species such as better tolerance to severe climatic factors in mountains or in extreme northern regions of Europe. The relatively short period of intensive vegetative growth (only in June and July) may also have the same explanation.

Although the reproductive success of *D. expansa* in terms of fertile fronds, both in natural (Rünk *et al.*, 2006) and experimental conditions, as well in number of spores, were not lower than of *D. carthusiana*, a low mean intragametophytic selfing rate of 0.34 (Soltis and Soltis, 1987) and thus low establishment ability may have an effect on the distribution frequency of the species. The lower vegetative growth of diploid *D. expansa* and hence lower competitive ability (Rünk *et al.*, 2004) and lower post-emergence growth compared to tetraploid *D. carthusiana* could be connected to the diploid origin and mating system (comparatively low intragametophytic selfing rate) of the species. The differences between diploid and tetraploid species may partly be based on higher levels of inbreeding depression in the case of diploid species (Masuyama and Watano, 1990). Tetraploid fern species are generally larger (Page, 2002), due to heterosis, and have higher rates of spore germination and faster growth rates (Kott and Peterson, 1974).

Considering that *D. dilatata* is a tetraploid, its potential growth ability should be as high as *D. carthusiana*. Still, according to the results of the present experiment, *D. dilatata* had slower leaf elongation rates of young sporophytes during the first growth period, specifically in July and August,

which resulted in shorter plants by the end of September. *Dryopteris dilatata*, compared to *D. expansa*, had taller and a faster increasing number of fronds. *Dryopteris dilatata* had a different growth strategy compared to the other two species. Growth of the longest frond of *D. dilatata* was intensive for only a very short time, in June during the first growth period, similar to *D. expansa*. By contrast *D. dilatata* had an intensive increase in the number of fronds during almost the whole growth period until October, an even longer duration than *D. carthusiana*. The ability of *D. dilatata* to maintain intensive vegetative growth of the longest frond for a longer time may be restricted by some climatic factor. The notable difference in the timing of these two parameters may be connected with the different type of parameters under discussion. Since the frond size is more plastic than the number of fronds, an increase in the number of the fronds was preferred by the trade-off between the two parameters. Consequently, that ability of *D. dilatata* to establish in local vegetation very probably depends on some climatic factor. In better weather conditions *D. dilatata* may grow larger than *D. expansa* in the first growth period (Rünk *et al.*, 2004) and have better post-emergence growth ability. The growth of the species may be slower in less ideal conditions, as in the first growth period and continued in the second of the present experiment. In the second growth period *D. dilatata* achieved the highest LER, had a larger biomass, more and longer fronds than *D. expansa*; however this may occur too late for the successful establishment of the specific cohort and as well for the species.

With regards to the reproductive parameters, *D. dilatata* had the lowest number of spores, the lowest number of fertile individuals and a lower relative number of fertile fronds, compared to the other species. The number of fertile fronds per fertile individual of *D. dilatata* was also the lowest among the three species, although the difference with *D. expansa* was not significant. Taken all together, those differences indicate that in given conditions, the reproductive success of *D. dilatata* might be the lowest. Not only may the unstable establishment abilities limit the distribution of *D. dilatata*, but also its comparatively low self-fertilization rate (only 19.2% gametophytes on soil and 35.2% on decomposed wood produced sporophytes; Seifert, 1992). Therefore a low establishment potential may contribute to the low frequency of this species in Estonia.

In conclusion, the relative population density of the three *Dryopteris* species is related to the relative establishment abilities of the species. *Dryopteris carthusiana* had the highest values of the length parameters of vegetative growth and growth rate in the first growth period and has the highest local population density, while *D. dilatata* and *D. expansa*, both with shorter fronds, shorter intensive growth periods and lower leaf elongation rates, have lower population densities.

Although the short time period of our observatory studies did not allow for any assessment of the dynamics of the distribution of *D. dilatata* in the region, the dynamic population structure (Rünk *et al.*, 2006) and high plasticity (Rünk and Zobel, 2007) of the species might indicate that those species have a good perspective to expand their distribution in the future.

Data made available in 2003 (Blamey *et al.*) has already shown expansion of the distribution of *D. dilatata* in Great Britain and Ireland during the last 40 years. Explanations for the distribution expansion may be the relatively young age of *D. dilatata* (allotetraploid, originated from *D. expansa* and *D. intermedia*), or expansion due to climate warming as already predicted (Bakkenes *et al.*, 2002).

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